

## Article

# A New Species of *Lycodapus* from the Emperor Seamount Chain, Northwestern Pacific Ocean (Teleostei: Zoarcidae) †

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**Abstract:** A new species, *Lycodapus imperatorius*, is described from the seamounts of the Emperor Ridge, North Pacific Ocean. The new species can be identified by its stout gill rakers, single interorbital pore, four preopercular and four mandibular pores, 95–99 vertebrae, numerous vomerine and palatine teeth, and *COI* mtDNA sequences. Although the new species is most similar to *L. endemoscotus* and *L. antarcticus* in morphology, the closest match to already published sequences was *Lycodapus fierasfer*, which is fairly different from the new species in terms of morphology. The incongruence between molecular and morphological inferences might be explained by the homoplastic nature of the morphological characteristics used for species delimitation in *Lycodapus*. The percent of genetic identity between the closest species of *Lycodapus* ranges from 95.4 to 98.6% in comparison with 99.5–100.0% between individuals of the same valid species. A key of the genus is amended to include the new species.

**Keywords:** deep-water fishes; submarine ridges; taxonomy; DNA barcoding; North Pacific

## 1. Introduction

The zoarcid genus *Lycodapus* Gilbert, 1891 was reviewed in [1,2], where there were twelve valid and one unnamed species defined; the latter was subsequently described as *L. antarcticus* [3]. This genus is very peculiar in the family due to its compressed head and body with loose naked skin, terminal mouth with oblique mouth gape, large gill opening, and head pore pattern [1]. Eleven of the thirteen species are known to be from the North Pacific Ocean, ranging from the Bering Sea in the south to the Sea of Okhotsk in the western North Pacific and to Panama in the eastern Pacific [4]. A single specimen of this genus was reported from the Emperor Seamounts as *Lycodapus* sp. [5], which was later reiterated in [6,7]. In April 2019, during a research cruise onboard R/V “Professor Kaganovsky” [8], the second specimen of an unidentified *Lycodapus* species was found

in a catch off the Emperor Seamount [9], where two other new deep-water species were recently discovered [10,11]. A thorough examination of these two specimens reveals their attribution to a new species, the description of which is an aim of the present paper.

## 2. Materials and Methods

The type specimens of the new species are housed in the Institute of Oceanology, Russian Academy of Sciences, Moscow (IORAS) and in the Museum of the A.V. Zhirmunsky National Scientific Center of Marine Biology, Far Eastern Branch of the Russian Academy of Sciences (MIMB). Catalog numbers and label data are presented under species description. The new species has been registered in ZooBank (urn:lsid:zoobank.org:act:321864B9-B477-48C1-8AAB-E3195562FF78).

Definitions of the morphological characteristics and measurements follow [1,12]. Rays in unpaired fins and vertebrae were counted from radiographs. In the description, the characteristics or values for the paratype, when different from the holotype, are enclosed in brackets. Counts that differed on opposite sides of the same specimen are separated by slash (/). Abbreviations used: R/V, research vessel; TL and SL, total and standard length, respectively.

The tissue samples used for genetic analysis are listed in Table 1. All tissue samples were fixed in volumes of 96% ethanol at least five times larger than the sample volume. Fixed samples were stored at  $-20\text{ }^{\circ}\text{C}$ ; ethanol was changed approximately one month after collection and again after one year. DNA was extracted using the Wizard SV 96 Genomic DNA Purification System (Promega Corporation, Madison, WI, USA) according to the manufacturer's manual. All molecular genetic studies (DNA extraction, polymerase chain reaction (PCR), PCR product purification, and nucleotide sequencing) were performed using standard molecular genetic techniques [13]. Cytochrome oxidase subunit I (*COI*) fragment was amplified with a primer complex of *VF2\_t1*, *FishF2\_t1*, *FishR2\_t1*, *FR1d\_t1* [13,14]. Amplification was conducted in a volume of 15  $\mu\text{L}$  with 90 ng total DNA, buffer x1, 2.5 mM  $\text{MgCl}_2$ , 0.2 mM dNTP, 0.5 mM of each primer, and 0.75  $\text{U } \mu\text{L}^{-1}$  Color Taq polymerase. Cycling consisted of 5 min at  $95\text{ }^{\circ}\text{C}$ , followed by thirty-five cycles of 30 s each at  $95\text{ }^{\circ}\text{C}$ , 45 s at  $52\text{ }^{\circ}\text{C}$ , 60 s at  $72\text{ }^{\circ}\text{C}$ , and a final extension for 12 min at  $72\text{ }^{\circ}\text{C}$ . All resulting amplicons were purified by ethanol precipitation [15].

Purified fragments were sequenced from both strands by Applied Biosystems BigDye Terminator v3.1. kit (Applied Biosystems, Foster City, CA, USA) with capillary electrophoresis on an ABI3500 Genetic Analyzer (*Thermo Fisher Scientific*, Waltham, MA, USA) in the VNIRO Laboratory of Molecular Genetics.

The resulting sequences were assembled in Geneious 6.5.0 (Biomatters, Auckland, New Zealand) [16] and aligned with the "ClustalW" built-in algorithm. The "postfix" was set to a maximum desired length after trimming of 565 bases, was trimmed more from the 3-end if necessary, and removed any leading and trailing ambiguous bases. Any sequences whose lengths were less than 565 bp were considered failures and were removed from the analysis. Next, the bidirectional sequences were assembled into contigs (with default settings: using dirty data algorithm, realigner, and prefer 3gap placement, as well as a 20-base minimum overlap and an 85% minimum match percentage). At this point, if any contig contained >2% ambiguities, those samples were also removed. Any remaining single-read sequences were used if their quality value was better than 98%.

The resulting sequences were subsequently translated into the necessary format to construct a haplotype network in the PopArt program (Allan Wilson Centre Imaging Evolution Initiative, Otago, New Zealand) [17]. The FaBox 1.41 converter was used to convert the fasta file to the format required for calculation [18]. A network of haplotypes was constructed based on the maximum parsimony method using TCS v.1.21 software (Computational Science Laboratory, Provo, UT, USA). DnaSP v. 5.10.01 software (University of Barcelona, Barcelona, Spain) was used for the analysis of the average number of nucleotide substitutions and the number of haplotypes in samples [19].

**Table 1.** Information about COI sequences and respective samples used for molecular analysis (NA—not available).

Group	Specimen Number	Species	Catalog ID of Voucher Specimens	GenBank Ascension Number	Capture Area	Voucher Specimen Depository/Source of COI Sequences
New species	1	<i>Lycodapus imperatorius</i> sp. nov.	IORAS 03641	OP759467	Emperor Seamounts	Institute of Oceanology, Moscow, Russia/NCBI
	28	<i>Lycodapus imperatorius</i> sp. nov.	MIMB 43527	ANGBF4848-12	Emperor Seamounts	Institute of Marine Biology, Vladivostok, Russia/[5–7], NCBI
Congeners	2	<i>Lycodapus antarcticus</i>	SC049627	FOAG506-08	Herd and McDonalds Islands	Australian Antarctic Division, Hobart, Australia/BOLD Systems
	3	<i>Lycodapus antarcticus</i>	SC049620	FOAG507-08	Herd and McDonalds Islands	Australian Antarctic Division, Hobart, Australia/BOLD Systems
	4	<i>Lycodapus antarcticus</i>	SC109846	FOAG558-08	Southern Ocean, Plateau North	CSIRO, Australian National Fish Collection, Hobart, Australia/BOLD Systems
	6	<i>Lycodapus endemoscotus</i>	NA	TZFPA064-06	British Columbia	Royal British Columbia Museum, Victoria, Canada/BOLD Systems
	7	<i>Lycodapus endemoscotus</i>	NA	TZFPA065-06	British Columbia	Royal British Columbia Museum, Victoria, Canada/BOLD Systems
	8	<i>Lycodapus fierasfer</i>	NA	ANGBF4849-12	No data	NA/Mined from GenBank, NCBI
	9	<i>Lycodapus fierasfer</i>	UW113553	FMV276-08	Oregon, USA	University of Washington, Fish Collection, Seattle, USA/BOLD Systems
	10	<i>Lycodapus fierasfer</i>	UW113567	FMV284-08	Oregon, USA	University of Washington, Fish Collection, Seattle, USA/BOLD Systems
	11	<i>Lycodapus fierasfer</i>	SIO 06-27	MFC401-08	Oregon, USA	Scripps Institution of Oceanography, San Diego, USA/BOLD Systems
	12	<i>Lycodapus fierasfer</i>	RBCM-006-028-018	TZFPA306-05	British Columbia	Royal British Columbia Museum, Victoria, Canada/BOLD Systems
	13	<i>Lycodapus fierasfer</i>	RBCM-006-028-019	TZFPA307-05	British Columbia	Royal British Columbia Museum, Victoria, Canada/BOLD Systems
	15	<i>Lycodapus mandibularis</i>	NA	TZFPA199-07	British Columbia	Royal British Columbia Museum, Victoria, Canada/BOLD Systems
	16	<i>Lycodapus mandibularis</i>	NA	TZFPA201-07	British Columbia	Royal British Columbia Museum, Victoria, Canada/BOLD Systems
	18	<i>Lycodapus pachysoma</i>	2009-1380	EATF164-10	Southern Ocean	Museum National d’Histoire Naturelle, Paris, France/BOLD Systems
	19	<i>Lycodapus pachysoma</i>	2009-0026	EATF403-10	Southern Ocean	Museum National d’Histoire Naturelle, Paris, France/BOLD Systems
	20	<i>Lycodapus pachysoma</i>	NA	TZFPA017-06	British Columbia	Royal British Columbia Museum, Victoria, Canada/BOLD Systems
	21	<i>Lycodapus pachysoma</i>	NA	TZFPA018-06	British Columbia	Royal British Columbia Museum, Victoria, Canada/BOLD Systems
	22	<i>Lycodapus pachysoma</i>	NA	TZFPA019-06	British Columbia	Royal British Columbia Museum, Victoria, Canada/BOLD Systems
	23	<i>Lycodapus pachysoma</i>	NA	TZFPA020-06	British Columbia	Royal British Columbia Museum, Victoria, Canada /BOLD Systems
	24	<i>Lycodapus pachysoma</i>	NA	TZFPA021-06	British Columbia	Royal British Columbia Museum, Victoria, Canada/BOLD Systems
	25	<i>Lycodapus pachysoma</i>	NA	TZFPA066-06	British Columbia	Royal British Columbia Museum, Victoria, Canada/BOLD Systems
	26	<i>Lycodapus pachysoma</i>	RBCM-006-034-021	TZFPA356-05	British Columbia	Royal British Columbia Museum, Victoria, Canada/BOLD Systems

Table 1. Cont.

Group	Specimen Number	Species	Catalog ID of Voucher Specimens	GenBank Ascension Number	Capture Area	Voucher Specimen Depository/Source of COI Sequences
	27	<i>Lycodapus pachysoma</i>	RBCM-006-034-022	TZFPB357-05	British Columbia	Royal British Columbia Museum, Victoria, Canada/BOLD Systems
	29	<i>Lycodapus</i> sp.	UW 150605	FMV581-11	Northeastern Pacific, USA	University of Washington, Fish Collection, Seattle, USA/BOLD Systems
	30	<i>Lycodapus</i> sp.	NA	GBMND68044-21	Southern Ocean	NA/Mined from GenBank, NCBI
	31	<i>Lycodapus</i> sp.	NA	GBMND68045-21	Southern Ocean	NA/Mined from GenBank, NCBI
	32	<i>Lycodapus</i> sp.	USNM 422332	MOP075-12	Pacific Ocean, Panama	Smithsonian Institution, National Museum of Natural History, Washington, USA/BOLD Systems
	33	<i>Lycodapus</i> sp.	USNM 421188	MOP643-12	Pacific Ocean, Costa Rica	Smithsonian Institution, National Museum of Natural History, Washington, USA/BOLD Systems
Sister group	34	<i>Bothrocara brunneum</i>	KU 28306	UKFBI299-08	California, USA	University of Kansas, Biodiversity Research Center, Lawrence, USA/BOLD Systems
	35	<i>Bothrocara brunneum</i>	RBCM-006-030-006	TZFPB324-05	British Columbia	Royal British Columbia Museum, Victoria, Canada/BOLD Systems
	36	<i>Bothrocara brunneum</i>	SIO 05-87	MFC324-08	California, USA	Scripps Institution of Oceanography, San Diego, USA/BOLD Systems
	37	<i>Bothrocara brunneum</i>	UW 119872	FMV471-11	Washington, USA	University of Washington, Fish Collection, Seattle, USA/BOLD Systems
	38	<i>Bothrocara hollandi</i>	NA	GBGC6548-09	Northern Sea of Okhotsk	NA/Mined from GenBank, NCBI
	39	<i>Bothrocara hollandi</i>	KC748099	GBGCA4726-13	Sea of Japan	Department of Marine Biology in Pukyong National University, Busan, Republic of Korea/Mined from GenBank, NCBI
	40	<i>Bothrocara hollandi</i>	NA	ANGBF56896-19	South Korea	NA/Mined from GenBank, NCBI
	41	<i>Bothrocara hollandi</i>	NA	ANGBF56898-19	South Korea	NA/Mined from GenBank, NCBI
	42	<i>Bothrocara hollandi</i>	NA	ANGBF56909-19	South Korea	NA/Mined from GenBank, NCBI
	43	<i>Bothrocara molle</i>	SIO 05-165	MFC333-08	California, USA	Scripps Institution of Oceanography, San Diego, USA/BOLD Systems
	44	<i>Bothrocara molle</i>	USNM 422430	MOP063-12	Pacific Ocean, Panama	Smithsonian Institution, National Museum of Natural History, Washington, USA/BOLD Systems
	45	<i>Bothrocara molle</i>	RBCM-006-034-003	TZFPB338-05	British Columbia	Royal British Columbia Museum, Victoria, Canada/BOLD Systems
	46	<i>Bothrocara molle</i>	RBCM-006-034-002	TZFPB337-05	British Columbia	Royal British Columbia Museum, Victoria, Canada/BOLD Systems
	47	<i>Bothrocara molle</i>	USNM 423188	MOP198-12	Pacific Ocean, Costa Rica	Smithsonian Institution, National Museum of Natural History, Washington, USA/BOLD Systems
	48	<i>Bothrocara zestum</i>	MIMB 22383	FERU090-13	Western Bering Sea	Institute of Marine Biology, Vladivostok, Russia/ BOLD Systems

Table 1. Cont.

Group	Specimen Number	Species	Catalog ID of Voucher Specimens	GenBank Ascension Number	Capture Area	Voucher Specimen Depository/Source of COI Sequences
	49	<i>Bothrocara zestum</i>	MIMB 22384	FERU094-13	Western Bering Sea	Institute of Marine Biology, Vladivostok, Russia/ BOLD Systems
	50	<i>Bothrocara zestum</i>	MIMB 22386	FERU092-13	Western Bering Sea	Institute of Marine Biology, Vladivostok, Russia/BOLD Systems
	51	<i>Bothrocara zestum</i>	MIMB 22384	GBGCA3018-13	Western Bering Sea	NA/Mined from GenBank, NCBI
	52	<i>Bothrocarina microcephala</i>	NA	GBGC6192-08	Northern Sea of Okhotsk	NA/Mined from GenBank, NCBI
	53	<i>Bothrocarina microcephala</i>	NA	GBGC6193-08	Northern Sea of Okhotsk	NA/Mined from GenBank, NCBI
	54	<i>Bothrocarina nigrocaudata</i>	NA	GBGC6194-08	Northern Sea of Okhotsk	NA/Mined from GenBank, NCBI
	55	<i>Bothrocarina nigrocaudata</i>	NA	GBGC6195-08	Northern Sea of Okhotsk	NA/Mined from GenBank, NCBI
	56	<i>Bothrocarina nigrocaudata</i>	NA	GBGC6196-08	Northern Sea of Okhotsk	NA/Mined from GenBank, NCBI
	57	<i>Bothrocarina nigrocaudata</i>	NA	GBGC6560-09	Northern Sea of Okhotsk	NA/Mined from GenBank, NCBI
	58	<i>Lycogrammoides schmidti</i>	NA	GBGC6555-09	Northern Sea of Okhotsk	NA/Mined from GenBank, NCBI
	59	<i>Lycogrammoides schmidti</i>	NA	GBGC6556-09	Northern Sea of Okhotsk	NA/Mined from GenBank, NCBI
	60	<i>Lycogrammoides schmidti</i>	NA	GBGC6557-09	Northern Sea of Okhotsk	NA/Mined from GenBank, NCBI
	61	<i>Lycogrammoides schmidti</i>	NA	GBGC6558-09	Northern Sea of Okhotsk	NA/Mined from GenBank, NCBI
	62	<i>Lycogrammoides schmidti</i>	NA	GBGC6559-09	Northern Sea of Okhotsk	NA/Mined from GenBank, NCBI
Outgroup	63	<i>Bathymaster signatus</i>	MIMB 22194	FERU014-11	Western Bering Sea	Institute of Marine Biology, Vladivostok, Russia/BOLD Systems

Data processing was performed, and genetic distances and percent identity were calculated using Geneious 6.0.5 software (Biomatters, Auckland, New Zealand) based on the Bayesian Inference method with *Bathymaster signatus* as the outgroup [5–7,20,21] with the use of a Substitution Model HKY85; 1,100,000 chain length; and 100,000 burn-in-length [22].

Data on the COI sequences of the outgroup and congeners of a new species (sister groups involved in an analysis for comparative purposes) were taken from the open NCBI (<https://www.ncbi.nlm.nih.gov/>, accessed on 3 November 2022) and BOLD Systems (<https://www.boldsystems.org/>, accessed on 3 November 2022) databases.

### 3. Results

#### *Lycodapus imperatorius* sp. nov.

##### Figure 1

urn:lsid:zoobank.org:act:321864B9-B477-48C1-8AAB-E3195562FF78



**Figure 1.** *Lycodapus imperatorius* sp. nov., holotype, IORAS 03641, 140 mm SL: (A) fresh caught, (B) after thawing.

**Holotype:** IORAS 03641, female, TL 144 mm, SL 140 mm, R/V “Professor Kaganovsky”, 11.04.2019, bottom trawl, haul 107, Lira Seamount, 36°48′08″–36°47′09″ N, 171°23′00″–171°23′05″ E, depth 643–649 m, DNA-sample 89, collector A.M. Orlov.

**Paratype:** MIMB 43527, female, TL 132 mm, SL 128 mm, R/V “TINRO”, 06.04.2010, bottom trawl, haul 75, Jingu Seamount, 38°43′01″ N, 171°07′05″ E, depth 806–822 m, collector A.A. Balanov.

**Diagnosis.** Identified by the stout gill rakers (gill raker ratio 58–66%), single interorbital pore, four preopercular and four mandibular pores, 95 to 99 vertebrae, 16 vomerine and 24–29 palatine teeth in females, upper rim of eye below dorsal contour of head, upper end of gill slit level to just above upper end of pectoral-fin base, and snout relatively long (32.1–35.2% of head length).

**Description.** Measurements shown in Table 2. Vertebrae 99 (17 + 82) [95 (16 + 79)]. Body elongate, tapering posteriorly, compressed laterally, slightly humped at nape. Dorsal and anal fins continuous, confluent with small truncate caudal fin. Dorsal-, anal-, and caudal-fin rays 101 [89], 83 [80], and 10 (2 + 4 + 4) in number, respectively. Dorsal-fin origin situated slightly closer to the base than to the tip of pectoral fin adpressed to body. First dorsal-fin pterygiophore inserted between fourth and fifth [fifth and sixth] neural spines. Longest dorsal-fin rays about as long as pectoral rays; longest anal-fin rays about 1.5 times shorter than those of dorsal fin. Pectoral fin small, narrow-based, rounded at tip, 3.3 [2.8] times in head. Pectoral-fin rays 9 [8], covered with loose transparent skin. Pelvic fins absent. Head moderate, 5.3 [5.4] times in SL, with dorsal contour concave before eyes. Eye lateral in position, not entering dorsal profile of head, 6.2 [5.2] times in head length. Interorbital space convex, slightly (1.2 [1.1] times) exceeding eye diameter in width. Nostril with slightly raised rim [tubular]. Mouth gape moderately large, oblique; upper jaw reaching to mid-eye. Symphyseal knob of lower jaw small, aciculate; mandibular joint forming a conspicuous triangular protrusion. Gill slit originating at level of upper end of pectoral-fin base or

just above it, extending forward to vertical of posterior third of eye. Gill rakers short and broad-based (length 1.5 times greater than width at base), with tips truncated, armed with small denticles (10–12 denticles per raker), 12 (2 + 10) [14–15 (2 + 12/2 + 13)] on first arch; relative gill raker ratio 58 [66]. Two pseudobranchial filaments.

**Table 2.** Measurements of *Lycodapus imperatorius* sp. nov.

Character	Holotype	Paratype
TL, mm	144	132
SL, mm	140	128
In % of SL		
Head length	18.9	18.6
Body depth	10.0	9.4
Body width	5.7	3.9
Predorsal distance	21.4	20.9
Preanal distance	36.4	35.9
Longest dorsal-fin ray	5.7	5.9
Longest anal-fin ray	3.9	3.9
Pectoral-fin length	5.7	6.6
Caudal-fin length	2.9	2.9
Snout length	6.1	6.6
Eye diameter	3.1	3.6
Interorbital width	3.6	3.9
Upper-jaw length	8.6	9.0
Eye to pectoral-fin base	9.3	9.9
Jaw to gill isthmus	9.3	10.0
Gill slit length	10.4	11.1
Upper end of gill slit to upper end of pectoral base	0	0.9
Upper pectoral base to dorsal midline	7.1	5.9
Length of fourth lower gill raker	0.5	0.6
Distance between 4th and 5th lower gill rakers	0.9	0.9
In % of head length		
Snout length	32.1	35.2
Eye diameter	16.2	19.3
Interorbital width	18.9	20.9
Upper-jaw length	45.3	48.1
Eye to pectoral-fin base	49.1	53.1
Jaw to gill isthmus	49.1	53.6
Gill slit length	54.7	59.4
Upper end of gill slit to upper end of pectoral base	0	5.0
Upper pectoral base to dorsal midline	37.7	31.4
Length of fourth lower gill raker	2.8	3.4
Distance between 4th and 5th lower gill rakers	4.9	5.0
Pectoral-fin length	30.2	35.6
Caudal-fin length	15.1	15.5

Jaw dentition villiform, arranged in bands, teeth in outermost row near the symphyses slightly enlarged and curved outward, more conspicuously on premaxilla. Vomerine and palatine teeth uniserial, pointed; those on vomer slightly longer, somewhat greater than the outermost curved teeth on premaxilla, arranged in broadly V-shaped series and slightly increasing in length posteriad (but hindmost tooth on both sides small). Palatine teeth nearly uniform in size. There are 16 vomerine and about 27/29 [24/26] palatine teeth.

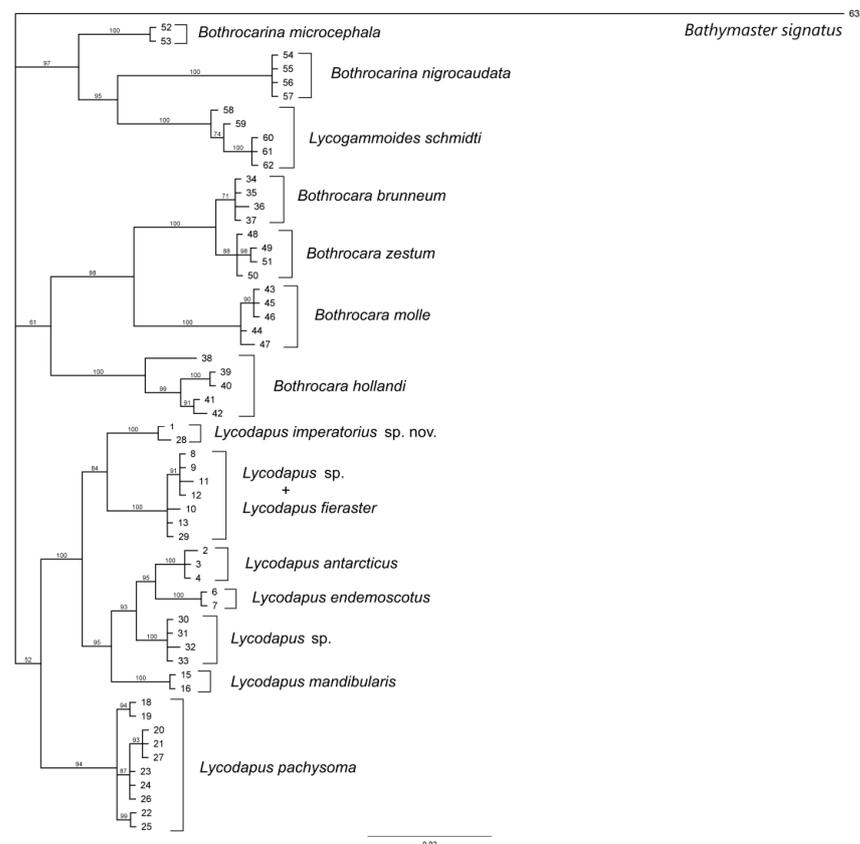
Pores in cephalic laterosensory system: supraorbital, 3 (nasal, preorbital, and postorbital pores); interorbital (coronal), 1; mandibular, 4; preopercular, 4. Infraorbital canal and pores absent. Free lateralis organs on side of body inconspicuous, discernible only in mediolateral line above gill opening and pectoral-fin base.

Skin naked, thin, movable. Anus close to anal-fin origin. Pyloric caeca absent.

Preserved specimens pale-colored with skin semitransparent, whole head and body densely peppered by black dotted melanophores on a diffuse brownish subcutaneous pigmentation becoming more pronounced caudally; dorsal and anal fins hyaline with rays peppered with small black melanophores becoming much denser caudally, where melanophores confluent to almost uniform blackish pigmentation along hindmost portions of dorsal and anal fins. Pectoral fin unpigmented. Branchiostegal membrane, orobranchial cavity and dorsal surface of tongue dotted with small blackish melanophores [uniformly dark in paratype]; gill arches and pseudobranchial filaments unpigmented. Peritoneum brownish to blackish, not solidly pigmented; stomach with longitudinal streaks of melanophores dorsally; intestine unpigmented. In fresh specimen, body was more brownish, darkened toward tail tip, and abdomen was bluish with partly translucent blackish peritoneum.

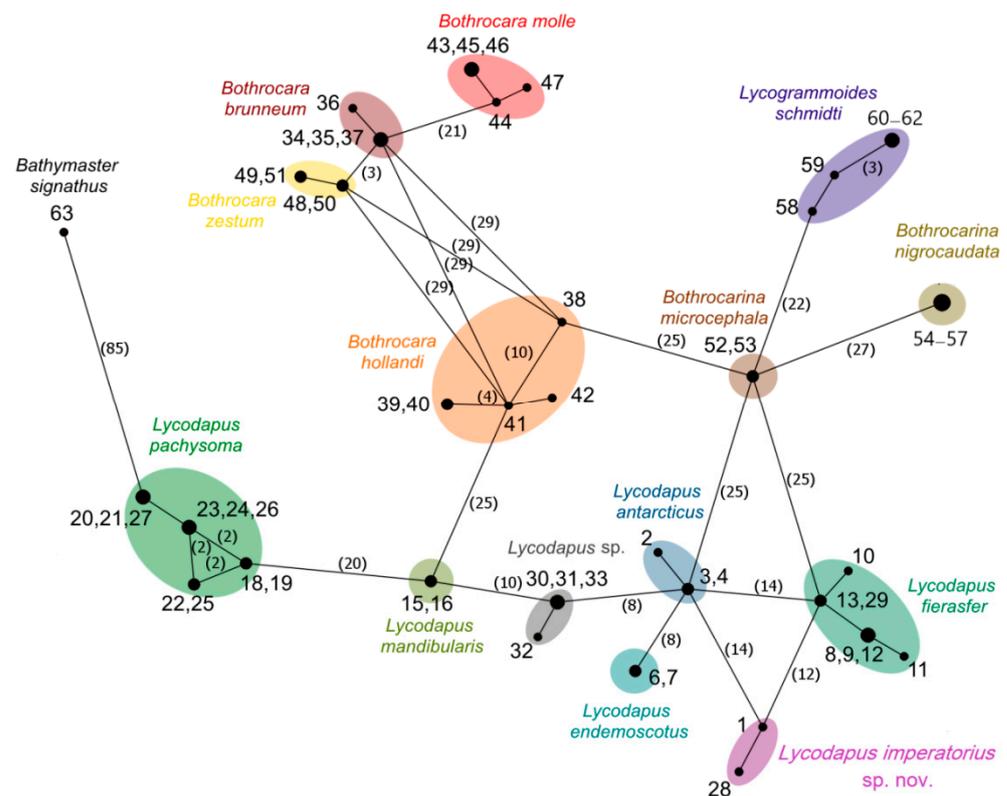
**Etymology.** The species name is given in reference to the type of locality of the species (Emperor Seamount Chain).

**Genetic analysis.** Molecular data indicate that the new species *Lycodapus imperatorius* sp. nov. seems genetically closer to *L. fieraster* from the northeastern Pacific Ocean than to *L. endemoscotus* from the same region, to which it is more morphologically similar (Figure 2). Moreover, *L. imperatorius* and *L. fieraster* form a separate clade on the phylogenetic tree, which is well-separated from the clade formed by *L. mandibularis* (northeastern Pacific Ocean), *L. endemoscotus* (northeastern Pacific Ocean), *L. antarcticus* (Southern Ocean), and the undescribed species *Lycodapus* sp. (records from Costa Rica to the Southern Ocean). The clade represented by *L. pachysoma* from the waters of British Columbia and the Southern Ocean is well-separated from these two clades.



**Figure 2.** Tree topology reconstruction of specimens of *Lycodapus imperatorius* sp. nov, its congeners, sister group, and outgroup based on the Bayesian Inference Substitution Model HKY85; 1,100,000 chain length; and 100,000 burn-in-length for mitochondrial cytochrome oxidase subunit I (COI) genes. Numbers beside each branch indicate bootstrap values. Numbers to the right of the branches correspond to the number of specimens in Table 1.

Phylogenetic relationships (Figure 3) testify that the new species is genetically closest to *L. fierasfer*, with which it has 97.4–97.8% genetic identity. A little more (97.3–97.6% identity) *L. imperatorius* is separated from *L. antarcticus*. It should be noted that the percent of identity between closest species of the genus *Lycodapus* ranges from 95.4 to 98.6%, while that between individuals of the same valid species amounts to 99.5–100.0%. The maximum % identity (98.5–98.6%) was observed between *L. antarcticus* and *L. endemoscotus*, as well as between *L. antarcticus* and the undescribed *L. sp.* (97.4–98.6%). The minimum % identity (96.0–96.6%) was recorded between *L. mandibularis* and *L. pachysoma*.



**Figure 3.** Phylogenetic relationships of *Lycodapus imperatorius* sp. nov. and allied species by COI mtDNA sequences. Numbers indicate haplotypes (see Table 1 for explanation), numbers of substitutions are given in brackets, size of black circles correspond to number of specimens.

#### 4. Discussion

When comparing the new species with its congeners in external features, *Lycodapus imperatorius* is easily confused with *L. endemoscotus* from the eastern North Pacific between 27 and 50° N [1]. The two species are almost identical in morphology except for the higher vertebral count in the new species (95–99 vs. 87–95 in *L. endemoscotus*) and relative position of the upper ends of gill slit and pectoral-fin base (these are more closely spaced in the new species, with the distance between them equal to 0–5.0% of the head length instead of 4.2–12.1% in *L. endemoscotus*). However, the percent of identity between *L. imperatorius* and *L. endemoscotus* is 96.9–97.1%, and these species fall into different clades on the phylogenetic tree (Figures 2 and 3).

Although *L. imperatorius* and *L. fierasfer* are the closest genetic relatives, these species are strikingly different from each other in morphology. The new species differs from *L. fierasfer* in the stout (vs. long) gill rakers (gill raker ratio 58–66% vs. 117–256% (usually 150% or more) in *L. fierasfer*), four (vs. three) mandibular and preopercular pores, single (vs. typically two) interorbital pore, and higher total and precaudal vertebral count (95–99 and 16 or 17 vs. 83–91 and 13–15). Such incongruence between the molecular and mor-

phological inferences might be explained by the homoplastic nature of the morphological characteristics used for the species delimitation in *Lycodapus*.

The new species is also similar, both morphologically and genetically, to *L. antarcticus* known circumglobally from the Southern Ocean. However, the new species can be separated from *L. antarcticus* by the longer snout (32.1–35.2% vs. 24.7–31.5% of head length), more numerous palatine teeth (24–29 vs. 6–23 in *L. antarcticus*), less numerous vertebrae (95–99 vs. 98–105 in *L. antarcticus*) [3,23], and 97.3–97.6% genetic identity. The new species differs from *L. leptus* from the Bering Sea by the presence of four normally developed preopercular pores (vs. three pores, often secondarily closed in adults), numerous palatine teeth (24–29 vs. 0–5), and a longer head (19% vs. 13–15% SL) [2]. The new species can be easily distinguished from the other short and stout gill-raker species (*L. mandibularis*, *L. microchir* and *L. pachysoma*) by its higher vertebral count (95–99 vs. 81–96, increasing in more northern populations of *L. mandibularis*; 75–85 in *L. microchir* and *L. pachysoma*) and further differs from *L. mandibularis* by the more numerous vomerine and palatine teeth (16 and 24–29 vs. 0–5 and 3–13, respectively) and by the eye not entering the dorsal profile of the head (vs. eye interrupts the concave dorsal profile in *L. mandibularis*) [2].

### 5. Key to Species of *Lycodapus*

(Modified from [2])

- 1A. Gill rakers on first gill arch very short and blunt; gill raker ratio less than 30% . . . . . 2
- 1B. Gill rakers stout to long; gill raker ratio more than 30% . . . . . 3
- 2A. Four preopercular pores; vomerine plus inner row of dentary teeth enlarged and not sexually dimorphic in adults; gill slit not extending above pectoral base (Strait of Juan de Fuca to Aleutian Islands) . . . . . *Lycodapus parviceps*
- 2B. Three preopercular pores; vomerine and dentary teeth small; gill slit extending slightly above pectoral fin base (Bering Sea) . . . . . *Lycodapus psarostomatus*
- 3A. Gill rakers of first gill arch, blunt and stout (pointed in young *L. mandibularis*), gill raker ratio usually 30 to 150% (rarely 170% in juveniles); when rakers of first arch are pressed downward against the arch, their tips usually lie close to and not beyond base of the adjacent raker down the arch; one median interorbital pore, four mandibular pores, four preopercular pores (except *L. leptus* has less than four preopercular pores) . . . . . 4
- 3B. Gill rakers of first gill arch, long, slender and pointed; gill raker ratio usually between 150 and 270%, if less than 150% the gill rakers are pointed and there are three preopercular pores; when rakers pressed downward against the arch, their tips usually lie closer to base of second raker down the arch than base of adjacent raker; a median or paired interorbital pore; three or four mandibular pores . . . . . 10
- 4A. Total number of vertebrae 75 to 82 (Antarctic and North Pacific Oceans) . . . . .  
. . . . . *Lycodapus pachysoma*
- 4B. Total number of vertebrae more than 82 . . . . . 5
- 5A. Total number of vertebrae 98 to 105; four preopercular pores, snout length less than 32% of head length (Antarctic waters) . . . . . *Lycodapus antarcticus*
- 5B. Total number of vertebrae 99 or less; if more than 96, then three preopercular pores or snout length greater than 32% of head length . . . . . 6
- 6A. Three preopercular pores, often secondarily closed in adults; total number of vertebrae, 94 to 99; palatine teeth, 0–5; head length 13 to 15% of SL (Bering Sea) . . . . .  
. . . . . *Lycodapus leptus*
- 6B. Four preopercular pores; total number of vertebrae, 79 to 99 (if more than 96 then palatine teeth numerous); head length 12 to 23% (usually more than 15%) of SL . . . . . 7
- 7A. Vomerine teeth 0 to 5; palatine teeth 3 to 13 (usually less than 10 on each side); upper rim of eye reaches level of dorsal profile of head; gill raker ratio about 65 to 165% (lower in adults) (total number of vertebrae 81 to 96; usually inhabits midwater at depths less than 700 m off western North America) . . . . . *Lycodapus mandibularis*

- 7B. Vomerine teeth 16 to 21 (reduced to 4 on some mature males); palatine teeth 8 to 29 on each side; upper rim of eye of adults below dorsal profile of head; gill raker ratio 49 to 106% . . . . . 8
- 8A. Total number of vertebrae 79 to 85 (Sea of Okhotsk and probably Bering Sea) . . . . . *Lycodapus microchir*
- 8B. Total number of vertebrae 87 to 99 . . . . . 9
- 9A. Total number of vertebrae 95 to 99; upper end of gill slit level to upper end of pectoral-fin base or only slightly above it; known from near-bottom layer at depths 643–822 m over the Emperor Seamounts . . . . . *Lycodapus imperatorius* sp. nov.
- 9B. Total number of vertebrae 87 to 95; upper end of gill slit well above from upper end of pectoral-fin base; inhabits depths of 933 to 2225 m off western North America, south of 50° N . . . . . *Lycodapus endemoscotus*
- 10A. Vomerine teeth absent; total number of vertebrae 73 to 84; precaudal vertebrae 14 or 15; a median interorbital pore; three preopercular pores (Sea of Okhotsk and western Bering Sea) . . . . . *Lycodapus derjugini*
- 10B. Vomerine teeth present; total number of vertebrae 77 or more; precaudal vertebrae 13 to 18; three or four preopercular pores . . . . . 11
- 11A. Usually two interorbital pores; three preopercular pores (sometime four in *L. australis*); three mandibular pores (sometimes four in *L. australis*); vertebrae 83 or more (if four preopercular or mandibular pores then 3 to 14 palatine teeth) . . . . . 12
- 11B. One interorbital pore; three preopercular pores (frequently four in *L. dermatinus*); four mandibular pores (frequently three in *L. dermatinus*); total number of vertebrae 76 to 87 . . . . . 13
- 12A. Lips with dark pigment; precaudal vertebrae 13 to 15; inhabits northeastern Pacific Ocean and Bering Sea) . . . . . *Lycodapus fierasfer*
- 12B. Lips without dark pigment; precaudal vertebrae 15 to 18; inhabits areas around Straits of Magellan) . . . . . *Lycodapus australis*
- 13A. Palatine teeth 2 to 26 (usually 6 to 18); vomerine teeth 3 to 19 (usually 5 to 12); total number of vertebrae 76 to 82; precaudal vertebrae 13 to 15 (northeast Pacific south of 56° N latitude) . . . . . *Lycodapus dermatinus*
- 13B. Palatine teeth 0–4 (usually 0–2); vomerine teeth 1–6 (usually 2–5); total number of vertebrae 80–87; precaudal vertebrae 15–17 (Bering Sea) . . . . . *Lycodapus poecilus*

## 6. Research Gaps and Future Directions

In conclusion, we outline some research gaps and possible directions for future taxonomic research of the studied species of the subfamily Lycodinae based on the conducted genetic analysis. Firstly, the presence of an undescribed *Lycodapus* species among the studied specimens is noteworthy, which is genetically closest to *L. endemoscotus* and *L. antarcticus*, with records in the waters of Costa Rica, Panama, and the Southern Ocean. The next step should be its morphological study, followed by a taxonomic description.

Genetic analysis revealed significant intraspecific variations in some *Lycodapus* species. For example, *L. pachysoma* has two clades on the phylogenetic tree, represented by specimens from the Southern Ocean (Nos. 18 and 19) and the waters of British Columbia (Nos. 20–27). Given such a disjunct distribution, it is possible to conclude with a high degree of probability that, in this case, we are dealing with two distinct species. At the same time, genetic analysis showed that there are also significant differences between specimens from the waters of British Columbia (Nos. 25 and 22 vs. the rest ones), which may indicate the presence of a cryptic species in this area. All of the above requires additional taxonomic studies.

Another interesting aspect is the high species diversity of the genus *Lycodapus* in the northeastern Pacific, which requires appropriate research aimed at identifying the center of speciation and ways of further dispersion of representatives of this genus.

So far, the records of the *Lycodapus* species in the northwestern Pacific are very rare, and they are limited to the waters of the southern Sea of Okhotsk and Eastern Kamchatka [4,24].

Since the taxonomic status of the captured specimens remains unclear, further morphological and genetic study of them seems quite relevant.

Among the genetically studied representatives of the genus *Bothrocarina*, *B. hollandi* stands out, previously referred to the genus *Allolepis*. Genetically, this species is closer to *Bothrocarina microcephala* and *Lycodapus mandibularis* than to its congeners (95.4–95.7% vs. 93.3–95.0% identity, respectively). These results require additional studies aimed at revising the taxonomic status of *B. hollandi*.

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